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Dental functional morphology predicts the scaling of chewing rate in mammals

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Abstract

How food intake and mastication scale to satisfy the metabolic needs of mammals has been the subject of considerable scientific debate. Existing theory suggests that the negative allometric scaling of metabolic rate with body mass is compensated by a matching allometric scaling of the chewing rate. Why empirical studies have found that the scaling coefficients of the chewing rate seem to be systematically smaller than expected from theory remains unknown. Here we explain this disparity by decoupling the functional surface area of teeth from overall surface area. The functional surface area is relatively reduced in forms emphasizing linear edges (e.g., lophodont) compared with forms lacking linear structures (e.g., bunodont). In forms with reduced relative functional surface, the deficit in food processed per chew appears to be compensated for by increased chewing rate, such that the metabolic requirements are met. This compensation accounts for the apparent difference between theoretically predicted and observed scaling of chewing rates. We suggest that this reflects adaptive functional evolution to plant foods with different fracture properties and extend the theory to incorporate differences in functional morphology.

Introduction

A recent study in biophysiology by Viro et al. (2017) highlighted that scaling in mastication and processing of food does not strictly follow fixed laws, but balances between physical, physiological and temporal limits. Ever since the scaling of chewing rates was established for ungulates (Fortelius 1985), a lot of empirical evidence on chewing rates has been gathered to support or clarify the theory (Fortelius 1985, Druzinsky 1993, Shipley et al. 1994, Gerstner and Gernstein 2008, Ross et al. 2009, Ungar 2014, Viro et al. 2017). While the theoretical scaling of chewing rate to body mass is expected to be -0.25, the empirical chewing rates have been found to vary mainly in the range -0.15 to -0.22. The exponents observed thus seem to be systematically smaller, implying faster actual chewing than the theoretical scaling coefficient would suggest. Here we address this disparity.

We propose that the key to resolving this disparity lies in the adaptive relationships between dental morphology and mechanical properties of foods. Even though teeth scale isometrically with body mass (see, e.g., a review by Ungar 2014), the working surface of teeth may scale in different ways depending on their functional morphology. Mammalian molars often have linear structures formed of enamel crests, which work as the primary instruments for breaking food during mastication. Such structures are on the surface, but they are closer to linear than to surficial, and therefore do not necessarily scale directly with area. Therefore, if teeth primarily contain blades the working surface of teeth would be disproportionally smaller than the whole surface accommodating the blades, and the working surface would scale allometrically.

Regardless of dental morphology, animals need to process the amount of food expected from their body mass according to metabolic scaling. Teeth with a smaller working surface could, all else

being equal, process the required amount of food by chewing it more times. This would explain why many empirical slopes of chewing rate scaling tend to suggest faster chewing than expected from overall tooth size.

Scaling of teeth and chewing rate with metabolism

The prevailing, if sometimes bitterly criticized, model for scaling¹ of chewing rates (Fortelius 1985) relates chewing rates to metabolism in the following way.

The metabolic rate scales as $M^{0.75}$ (Kleiber 1932). While empirically observed exponents vary to an extent from group to group and depending on how the basal metabolic rates are controlled, "it seems to be a very general rule that the minimal metabolic rates of related animals are about proportional to (body mass)^{3/4}" (Alexander 1999). To satisfy this need the daily food intake must scale as $M^{0.75}$. As far as is known, oral volume and bite size of food scale approximately as M^1 (Clutton-Brock & Harvey 1983, Pretorius et al. 2016). Larger animals have lower energy needs per unit of body mass. Yet with each bite they intake the amount of food that is proportional to their body mass. The metabolic requirements balance out via chewing, since larger animals chew more slowly (Fortelius 1985) and therefore process fewer mouthfuls per unit of feeding time. A constant chewing rate across all body sizes does not even seem to be feasible due to biophysical constraints (Virost et al. 2017).

Based on pilot data and logical reasoning, Fortelius (1985) suggested that chewing rates should scale as $M^{-0.25}$. The argument is that since teeth scale as M^1 , and since food is 3-dimensional, the amount of food processed by each chew of ideal, isometric teeth of the same shape should also scale as M^1 , regardless of the original size of the individual food items ingested. The metabolic rate requirements per unit time of feeding are then satisfied as food processed per one chew multiplied by the chewing rate (the number of chews per time unit): $M^{-0.25}M^1 = M^{0.75}$.

Although largely unnecessary for the present argument, the model described above also fits other core scaling observations. If one chew results in an isometric volume of isometric particles, the number of chews *per mouthful* of food has to be constant across sizes, thus it should scale as M^0 . Furthermore, the number of mouthfuls of food needed to satisfy daily energy need will scale as $M^{0.75}$, and thus the number of chews *per day* will scale as $M^{0.75}M^0/M^1 = M^{-0.25}$. Since the number of chews per day and the chewing rate (speed) both scale as $M^{-0.25}$, the amount of time spent on chewing per day must be constant: $M^{-0.25}/M^{-0.25} = M^0$. This mechanism allows organisms to satisfy their metabolic needs within the 24 hours of a day, independently of their body size.

On a daily basis larger animals make fewer chews in relation to their body mass, but they live longer. The lifespan of mammals scales as $M^{0.25}$ (Linstedt and Calder 1981). Since the number of

¹ Scaling relationships are typically modeled as exponential equations: $E = aM^b$, where M is the body mass, E is the variable of interest (e.g. metabolic rate), and a and b are the model coefficients. In the logarithmic form of the same equation b is the slope and a is the constant, the latter is often omitted from the discussion. If $b=1$ then scaling is isometric meaning that E increases in proportion to M . If $b>1$ then scaling is positively allometric meaning that E increases faster than M . If $b<1$ then scaling is negatively allometric meaning that E increases slower than M , which is the case, for example, for the relation between metabolic rates and body mass. If $b=0$ then E is constant for all M . Some authors adjust regression models phylogenetically (Felsenstein 1985); however, such an adjustment assumes that evolution of traits is random following the Brownian motion model, and overestimates the impact of origin of a trait over natural selection (Felsenstein 1985, Westoby et al. 1995). Assuming that the relationship between traits and the occurrence of individuals in the environment is active and rapid, we use the ordinary least squares for parameter estimation. The rate of evolutionary change is completely irrelevant for this argument.

chews per day scales as $M^{-0.25}$, the number of chews per lifetime turns out to be constant $M^{0.25}M^{-0.25} = M^0$. Therefore, while teeth increase in proportion to the body size, the number of chews over lifetime, in principle, does not. Even though food is 3-dimensional, the surface of teeth that contacts food is 2-dimensional, as observed by Gould (1975). Since one mouthful of food scales as M^1 and the surface of teeth scales as $M^{2/3}$, the food-tooth contact per one chew scales as $M^1/M^{2/3} = M^{1/3}$. This implies that the wear rate of teeth per one chew must scale as $M^{1/3}$. Since the volume of teeth scales as M^1 , their height accordingly scales as $M^{1/3}$. As teeth wear in relation of their height, a tooth of height $M^{1/3}$ that wears at a rate $M^{1/3}$ will last for M^0 chews, just enough for the lifetime.

The question of how dental wear occurs during the interaction between dental tissues with each other and with particles in the food is also largely orthogonal to the main argument. Suffice it to say that, conditioned on diet, tooth wear is expected to be independent of body size. To the best of our knowledge, no evidence exists to suggest that those processes would depend systematically on body size.

How dental functional morphology relates to the breakage properties of foods

The scaling model theoretically explains why chewing rates are expected to scale as $M^{-0.25}$. Now we can proceed with the question why empirically observed scaling of chewing rates tends to be different. A hint comes from Lucas (2004), who argued from the perspective of fracture theory that "the working surface areas of teeth that fracture and fragment food particles will be proportional to $M^{0.5}$ " (p. 143). Importantly, Lucas makes a distinction between plastic and elastic fracture of foods. Plastic foods deform before cracking when force is applied. A simple example of plastic behavior would be chewing gum. Fully elastic foods instead respond to force instantaneously by cracking. A nut would be a simple example of elastic food. Lucas argues (p. 95) that only few plant or animal tissues display plastic deformation, although later (p. 163) he mentions that fruits become almost completely plastic at ripeness.

Lucas' argument for $M^{0.5}$ scaling of the *working surface* of teeth is developed for elastic foods. Reasoning from the biomechanical perspective of how energy propagates through a crack, he concludes that cracking of larger particles requires allometrically less force. He further argues that in case of *elastic food* the breakage area of tooth-food particle contacts cannot increase at a faster rate than the scaling of bite forces, which he shows to scale as $M^{0.5}$. Later in the book (p. 163) Lucas hints that for *fully plastic food*, at the opposite end of the idealized spectrum, the working surface should be isometric, which implies scaling of the working surface as $M^{0.67}$.

In practice many foods may be neither fully plastic nor fully elastic, but somewhere in between. In such a case, it would be reasonable to expect the working surface of teeth to scale empirically between $M^{0.67}$ and $M^{0.5}$. Following the scaling model of Fortelius (1985) we argue that food particles need to be broken into the same size in relation to tooth size (and ultimately body size), no matter whether food is plastic, elastic or in between. Assuming that this is the case, Table 1 tabulates what would be the expected chewing rate to satisfy the metabolic need of $M^{0.75}$ for different types of food. We can immediately see that the expected chewing rates from fully plastic to fully elastic food closely resemble empirical rates reported in the literature. Since, following Lucas' arguments, the working surface of teeth breaking elastic food would need to be smaller than breaking plastic food, all else being equal less food would be processed by one chew in case of elastic food. The compensation to satisfy the expected metabolic rate could come from chewing

more times instead. Therefore, we expect that for more elastic food chewing rates will be faster.

Table 1. Chewing rates needed to satisfy the metabolic rate of $M^{0.75}$ at different scaling of working surfaces of teeth. The computation assumes that the volume of food captured between the teeth is the same but the amount processed depends on the morphology. The amount of food processed per chew would then scale as the working surface of the tooth times food height, which scales as $M^{1/3}$. The expected chewing rate would then be the metabolic rate ($M^{0.75}$) divided by the amount of food processed per chew.

Type of food	Working surface of a tooth	Food processed per chew	Expected chewing rate
Fully plastic	$M^{0.67}$	M^1	$M^{-0.25}$
	$M^{0.6}$	$M^{0.93}$	$M^{-0.18}$
	$M^{0.55}$	$M^{0.88}$	$M^{-0.13}$
Fully elastic	$M^{0.5}$	$M^{0.83}$	$M^{-0.08}$

Functional dental morphology successfully predicts scaling of chewing rate

Chewing different types of food requires different dental morphology. Animals chewing on grass tend to have flat and high crowned teeth, while animals chewing on leaves and other browse tend to have lophed teeth which are not necessarily high crowned. Lignified plant foods are elastic, as can be inferred for example from data in Bernays (1991), and are primarily fractured by blades (Lucas 2004, p. 120). As argued in the previous section, for most elastic food the working surface area should be the smallest in relation to the overall tooth size (Table 1).

More specifically, with lophed teeth the major food processing work is done by the blades. It is obvious upon inspection that this results in the working surface of a lophodont tooth being much smaller than the overall surface. The extra surface is needed to support the lophs, which actually do the cutting. Lophed teeth would accordingly have the smallest working area in relation to the tooth size, and would therefore have the fastest chewing rates. We empirically analyze the relationship between chewing rates and dental morphology using the chewing data from Gerstner and Gerstein (2008) complemented by functional crown type data using the scoring scheme from Zliobaite et al. (2016). The crown type scores are listed in Table S4 in the Appendix.

The dental trait scoring scheme captures durability of teeth and their functional properties according to a tradition of dental functional morphology reaching back to Cuvier and Aristotle (Fortelius 1990). We use three traits that describe teeth in terms of their functional properties: presence of acute lophs, obtuse lophs and occlusal topography (flat or non flat). Lack of lophs would generally indicate fruit eaters and omnivores (bunodont teeth), presence of obtuse lophs in combination with flat occlusal topography would indicate grazers (plagiolophodont teeth), while presence of lophs, especially acute lophs, and non-flat topography would indicate browsers or mixed feeders (lophodont teeth). We expect bunodonts to feed on the most plastic food (fruits), we expect grazers' food to be semi-elastic and browsers' food to be the most elastic. Therefore, we expect bunodonts to have their chewing rates the closest to the baseline $M^{-0.25}$, and browsers to have the fastest chewing rates, close to the limit of $M^{-0.16}$ suggested by Virot et al. (2017).

The wear of herbivore teeth is not only a matter of damage to an optimal shape, but more typically the process by which the functional shape is generated and maintained (Fortelius 1985b, Janis and Fortelius 1988). Even though the appearance of the occlusal surface may change substantially with wear (see e.g. Anders et al. 2011 for detailed discussion), the functionally critical aspects have been found to be surprisingly robust to such change until very late stages (Fortelius 1985a, Fortelius & Solounias 2000, King et al. 2005). We do not, however, expect chewing rates to change

in response to wear stage, because chewing rates are governed by biomechanical processes which are constrained by the body size (Virost et al. 2017). The variable that is more likely to change at the stage when teeth are heavily worn is the number of chews per mouthful (Chen 2009), or even more likely, the animal would swallow larger particle sizes (Mishellany-Dutour 2008) delegating more food processing work to the guts. Chewing rates as well as the length of chewing vary from individual to individual and in relation to food properties as well as circumstances and time available for chewing (Chen 2009), yet our goal is to analyze broad patterns at the species level.

We analyze four orders of large herbivores for which crown type scores are available: Artiodactyla, Perissodactyla, Proboscidea and Primates. The primarily insectivorous primates of less than 1 kg body weight (Fleagle 1988) are analyzed separately. They exhibit the same scaling relationship as the rest but transposed, with the same exponent but a higher constant. This leaves 72 species of large herbivorous mammals for the main analysis. The analysis excludes carnivorans, including omnivorous taxa such as bears, but includes omnivorous ungulates and primates as well as insectivorous primates, which share the same basic design of the chewing apparatus with herbivorous ungulates.

Figure 1 visualizes scaling of chewing cycle duration with body mass for different groups defined by functional morphology of teeth. The scaling results obtained by ordinary least squares fit² are given in Table 2, converting all results to chewing rate. Summary statistics of the fits as well as alternative slopes obtained by reduced major axis fit are given in Tables S1-S3 and Figure S1 in the Appendix.

We can see from the table that, as expected, forms lacking lophs have the slowest chewing rates, forms with obtuse lophs and flat occlusal surfaces are in the middle, while lophed forms with a non-flat occlusal surface have the fastest chewing rates, presumably to compensate for underscaling of the working surface relative to the whole surface.

The focus is on how relationship between body size and chewing rates is affected by the dimensionality of occlusal geometry. Under our reasoning, each occlusal class is its own entity with its characteristic scaling. In reality, these classes differ in their body size ranges, so that comparisons of absolute chewing rates across classes have complicated interpretations affected by many factors not considered here. Even though the three main classes (bunodonts, plagiolophodonts and lophodonts) have different ranges and distribution of body masses, the regression lines cross at around 40kg body mass, as plotted in Figure 2, suggesting a baseline body mass at which absolute chewing rates of different occlusal geometry coincide. Of all the large herbivores in our analysis only about 1/3 are below this body mass (the medium body mass is around 65kg), therefore, for medium and large sized animals lower working surface of teeth (lophodonts) relates to faster absolute chewing rates, which all else being equal would presumably compensate for the deficit of working surface.

² Historically, empirical relationships between body mass and chewing rates have been analyzed using reduced major axis (RMA) and ordinary least squares (OLS) fits interchangeably. We use OLS as the primary model, since it is more justified when biologically asymmetric relationship is modelled (Smith 2009), such as the chewing rate being dependent on body mass. Complementary analysis using RMA is presented in the Appendix (Supplementary material).

Table 2. Empirical scaling of chewing rates in groups of species by teeth morphology, ordinary least squares fit. Fit statistics can be found in Table S1 in the Appendix.

Group	Lophs	Occlusal topography	Implied diet	Implied properties	Empirical scaling of chewing rates
All large herbivores	Yes or no	Any	Any	Any	$M^{-0.196}$
All with lophs	Yes	Any	Grass or leaves	Elastic to semi-elastic	$M^{-0.173}$
Bunodonts	No	Any	Fruits and similar	Plastic	$M^{-0.246}$
Plagiolophodonts and similar	Yes (obtuse)	Flat	Mostly grass	Semi-elastic	$M^{-0.207}$
Lophodonts and similar	Yes	Non-flat	Leaves and similar	Elastic	$M^{-0.155}$
Small Primates	No	Non-flat	Insects	Plastic	$M^{-0.249}$

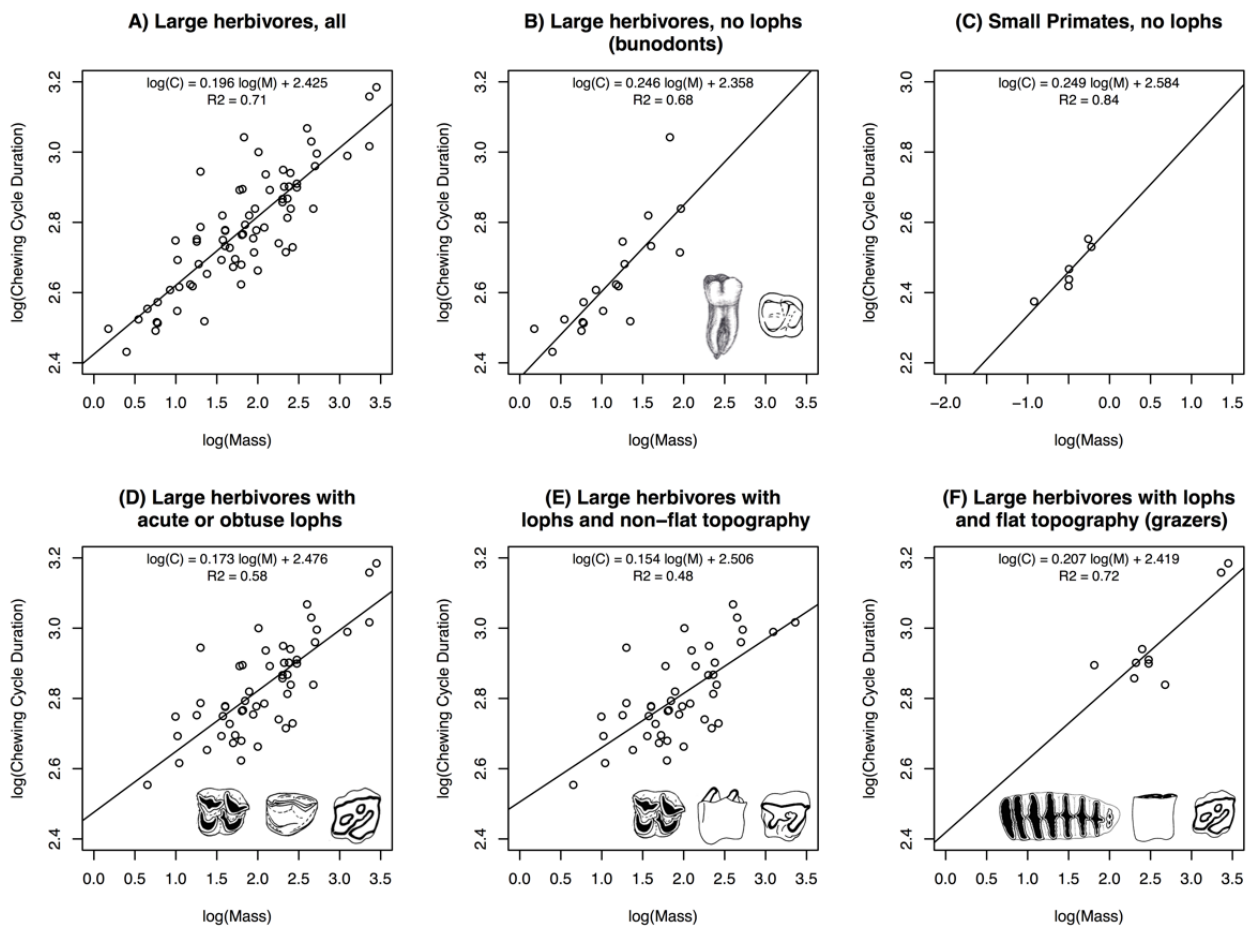


Figure 1. Scaling of chewing cycle duration with body mass, ordinary least squares fit. (A) Large herbivores (body mass more than 1 kg) of orders Artiodactyla, Perissodactyla, Proboscidea and Primates with all dental crown types, the line indicates ordinary least squares fit, the regression equation and the coefficient of determination (R^2) indicating model fit are given on the plot; (B) regression fit only on those large herbivores that have no lophs; (C) Small Primates (body mass less than 1kg), none have lophs; (D) regression fit only on those large herbivores that have lophs; (E) regression fit only on those large herbivores that have lophs and *non-flat* occlusal topography; (F) regression fit on those large herbivores that have lophs and *flat* occlusal topography. Tooth images are from Fortelius (1981), Thenius (1989) and public domain, tooth images are not to scale.

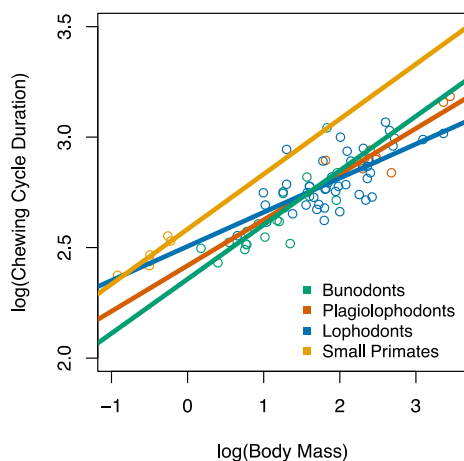


Figure 2. Intersection of regression line for different classes of occlusal geometry, ordinary least squares fit.

Discussion and conclusion

Our results explain the long-observed mismatch between theory and observed chewing rates. Lumping all herbivores, or all forms with lophodonts, gives allometric coefficients of the kind commonly reported in the literature, around or just below -0.2 (Fortelius 1985, Druzinsky 1993, Shipley et al. 1994, Gerstner and Gernstein 2008, Ross et al. 2009, Ungar 2014, Viot et al. 2017). When the species are sorted by occlusal morphology, corresponding to our argument about the relative size of the working surface, we observe the full spectrum from the theoretically expected -0.25 down to the lower limit of about -0.16 suggested by Viot et al. (2017). The theoretically predicted exponent of -0.25 is found in forms lacking lophodonts (bunodont herbivores and insectivorous primates), where the functional surface equals the entire occlusal surface.

There are in principle multiple ways in which the scaling of the functional occlusal surfaces could be adjusted to the metabolic needs. The surfaces themselves could for example be scaled up, the duration of chewing could be increased, or the chewing rate could be increased. To a first approximation it appears that the last of these is the predominant evolutionary solution. There is a certain amount of confusion about the role of dental size in functional evolution, arising from a general failure to make a distinction between the functional surface and the overall (basal) surface of teeth. Kay (1975a) actually came close to making that distinction when he observed that leaf-eating primates have larger molars for the same body size as compared to frugivorous primates (that do not have shearing crests on their molars) and that the scaling relationships depend on diet and morphology. Yet this line of reasoning appears to have been lost.

Substantially increasing the functional surface area would require correspondingly increased jaw size and muscle power (Turnbull 1970), while the increase in chewing duration could come up against ecological limits. Compared with these, increasing the rate of chewing appears easier, since it is known that animals are able to vary their chewing rate within certain physiological limits (Viot et al. 2017).

Our results suggest that the differences observed in chewing rates are explained by the breakage characteristics of different foods. Different kinds of foods that large mammals eat do indeed have different fracture characteristics, among which plasticity and elasticity are frequently mentioned. Plasticity is the property of a material to deform irreversibly, and elasticity is the property to deform reversibly. The conventional terms of functional dental research, such as cutting, shearing, grinding, crushing, represent attempts of researchers to capture their intuitive understanding of

the principles of oral comminution. In principle, two kinds of processes are implied: either the food is compressed or it is partitioned. Here we have assumed a gradient from one to the other, roughly corresponding to the gradient from plastic to elastic.

Several authors, including Kay (1975b) and Fortelius (1986), have argued that the relationship between tooth size and body size cannot be fully understood without considering diet in the equation, but a physiological explanation and biomechanical context to do so has been largely lacking. Here we propose that the variability in chewing rates that is observed can be explained by considering how dental functional morphology has been tailored to different diets by functional adaptation. Different occlusal morphologies result in different ratios of the functional surface to the overall surface of teeth. When working surface does not scale with the overall surface of teeth and size of the animal, increased chewing rate appears to act as a compensation mechanism.

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References

- Alexander, R. M. (1999). *Energy for animal life*. Oxford University Press.
- Anders, U., von Koenigswald, W., Ruf, I. and Smith, H. B. (2010). Generalized individual dental age stages for fossil and extant placental mammals. *Paläontologische Zeitschrift* 85:321-339.
- Bernays, E. (1991). Evolution of Insect Morphology in Relation to Plants. *Philosophical Transactions: Biological Sciences* 333 (1267), 257-264.
- Chen, J. (2009). Food oral processing—A review. *Food Hydrocolloids* 23, 1-25.
- Clutton-Brock, T. H. and Harvey, P. H. (1983). The functional significance of variation in body size among mammals. In J. F. Eisenberg and D. G. Kleiman (eds.): *Advances in the Study of Mammalian Behavior. Special Pub. Amer. Soc. Mammal.*, 632-663.
- Druzinsky, R. E. (1993). Time allometry of mammalian chewing movements, chewing frequency scales with body mass in mammals. *Journal of Theoretical Biology* 160, 427-440.
- Felsenstein, J. (1985). Phylogenies and the Comparative Method. *The American Naturalist* 125 (1), 1-15.
- Fleagle, J. G. (1988). *Primate Adaptation and Evolution*. Elsevier.
- Fortelius, M. (1981). Functional aspects of occlusal cheek-tooth morphology in hypsodont non-ruminant ungulates in Proc. of International Symposium on Concept and Method in Palaeontology, Barcelona. pp. 153–162.
- Fortelius, M. (1985a). The functional significance of wear-induced change in the occlusal morphology of herbivore cheek teeth, exemplified by *Dicerorhinus etruscus* upper molars. *Acta Zool. Fennica* 170: 157-158.
- Fortelius, M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica* 180:1-76.
- Fortelius, M. (1986). Isometric scaling of mammalian cheek teeth is also true metabolic scaling. In Russell, D.E.; Santoro, J.-P.; Sigogneau-Russell, D. (eds.): *Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986. Mémoires du Muséum national d'Histoire naturelle, Paris, Série C*, 53:459-462.

- Fortelius, M. (1990). The mammalian dentition, a 'tangled' view. *Netherlands Journal of Zoology* 40 (1/2), p. 312-328.
- Fortelius, M., and Solounias, N. (2000). Functional characterization of ungulate molars using the abrasion-attribution wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates*, 1-36.
- Gerstner, G. E. and Gerstein, J. B. (2008). Chewing rate allometry among mammals. *Journal of Mammalogy* 89, 1020-1030.
- Gould, S. J. (1975). On the Scaling of Tooth Size in Mammals. *American Zoologist* 15 (2), 351-362.
- Janis, C. M. and Fortelius, M., (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews (Cambridge)* 63, 197-230.
- Kay, R. F. (1975a). The functional adaptations of primate molar teeth. *Am J Phys Anthropol.* 43(2), 195-216.
- Kay, R. F. (1975b). Allometry and early hominids -- comment. *Science* 189, 63-63.
- King, S.J., Arrigo-Nelson, S.J., Pochron, S.T., Semperebon, G.M., Godfrey, L.R., Wright, P.C., Jernvall, J., 2005. Dental senescence in a long-lived primate links infant survival to rainfall. *Proc. Natl. Acad. Sci.* 102, 16579e16583.
- Kleiber, M. (1932). Body size and metabolism. *Hilgardia* 6, 315-351.
- Linstedt, S. L. and Calder, W. A. (1981). Body size, physiological time and longevity of homeometric animals. *The Quarterly Review of Biology* 56(1), p. 1-14.
- Lucas, P. W. (2004). Dental Functional Morphology: How Teeth Work. Cambridge: Cambridge University Press.
- Mishellany-Dutour, A., Renaud, J. Peyron, M. A., Rimek, F. and Woda, A. (2008). Is the goal of mastication reached in young dentates, aged dentates and aged denture wearers? *British Journal of Nutrition* 99(1):121-8
- Pretorius, Y., de Boer, W. F., Kortekaas, K., van Wijngaarden, M., Grant, R. C., Kohi, E. M., Mwakiwa, E., Slotow, R., Prins, H. H. T. (2016). Why elephant have trunks and giraffe long tongues: how plants shape large herbivore mouth morphology. *Acta Zoologica* 97(2), p. 246-254.
- Ross C. F., Washington R.L., Eckhardt A., Reed D.A., Vogel ER, Dominy N.J., Machanda Z.P. (2009). Ecological consequences of scaling of chew cycle duration and daily feeding time in Primates. *Journal of Human Evolution* 56(6):570-85.
- Shipley, L. A., Gross, J. E., Spalinger, D. E., Hobbs, N. T. and Wunder, B. A. (1994). The Scaling of Intake Rate in Mammalian Herbivores. *The American Naturalist* 143 (6), 1055-1082.
- Smith, R. J. (2009). Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology* 140(3):476-86.
- Thenius, E. (1989). Zahne und gebiß der saugetiere in Handbook of Zoology, Mammalia, eds. Niethammer J, Schliemann H, Starck D. (Walter de Gruyter, Berlin) Vol. VIII, pp. 1-513.
- Turnbull, W. D. (1970): Mammalian masticatory apparatus. Field Museum Press.
- Ungar, P. (2014). Dental Allometry in Mammals: A Retrospective. *Annales Zoologici Fennici* 51(1-2):177-187.
- Virost, E., Ma, G., Clanet, C. and Jung, S. (2017). Physics of chewing in terrestrial mammals. *Scientific Reports* 7, 43967.
- Westoby, M., Leishman, M. R., Lord, J. M. (1995). On misinterpreting the 'phylogenetic correction'. *Journal of Ecology* 83(53), 1-534.
- Zliobaite, I., Rinne, J., Toth, A., Mechenich, M., Liu, L., Behrensmeyer, A.K., Fortelius, M. (2016). Herbivore teeth predict climatic limits in Kenyan ecosystems. *PNAS* 113(45), 5 12751-12756.

Appendix

Table S1 presents summary statistics for ordinary least squares fit. Tables S2 and S3, as well as Figure S1 present reduced major axis fit. Table S4 gives the dataset used for the analysis.

Table S1. Empirical scaling of chewing rates in groups of species by teeth morphology, ordinary least squares, summary statistics.

Group	Slope	St. error for the slope	CI 95% for the slope	R ² of the log-fit	Sample size
All large herbivores	0.196	0.015	[0.166,0.226]	0.71	72
All with lophs	0.173	0.020	[0.132,0.214]	0.58	53
Bunodonts	0.246	0.041	[0.160,0.332]	0.68	19
Plagiolophodonts and similar	0.207	0.049	[0.091,0.323]	0.72	9
Lophodonts and similar	0.155	0.024	[0.105,0.204]	0.48	44
Small Primates	0.249	0.055	[0.097,0.401]	0.84	6

Table S2. Empirical scaling of chewing rates in groups of species by teeth morphology, reduced major axis fit.

Group	Lophs	Occlusal topography	Implied diet	Implied properties	Empirical scaling of chewing rates
All large herbivores	Yes or no	Any	Any	Any	M ^{-0.232}
All with lophs	Yes	Any	Grass or leaves	Elastic to semi-elastic	M ^{-0.226}
Bunodonts	No	Any	Fruits and similar	Plastic	M^{-0.298}
Plagiolophodonts and similar	Yes (obtuse)	Flat	Mostly grass	Semi-elastic	M^{-0.244}
Lophodonts and similar	Yes	Non-flat	Leaves and similar	Elastic	M^{-0.222}
Small Primates	No	Non-flat	Insects	Plastic	M ^{-0.272}

Table S3. Empirical scaling of chewing rates in groups of species by teeth morphology, reduced major axis, summary statistics.

Group	Slope	CI 95% for the slope	R ² of the log-fit	Sample size
All large herbivores	0.232	[0.204,0.264]	0.71	72
All with lophs	0.226	[0.189,0.271]	0.58	53
Bunodonts	0.298	[0.224,0.396]	0.68	19
Plagiolophodonts and similar	0.244	[0.154,0.386]	0.72	9
Lophodonts and similar	0.222	[0.178,0.277]	0.48	44
Small Primates	0.272	[0.160,0.464]	0.84	6

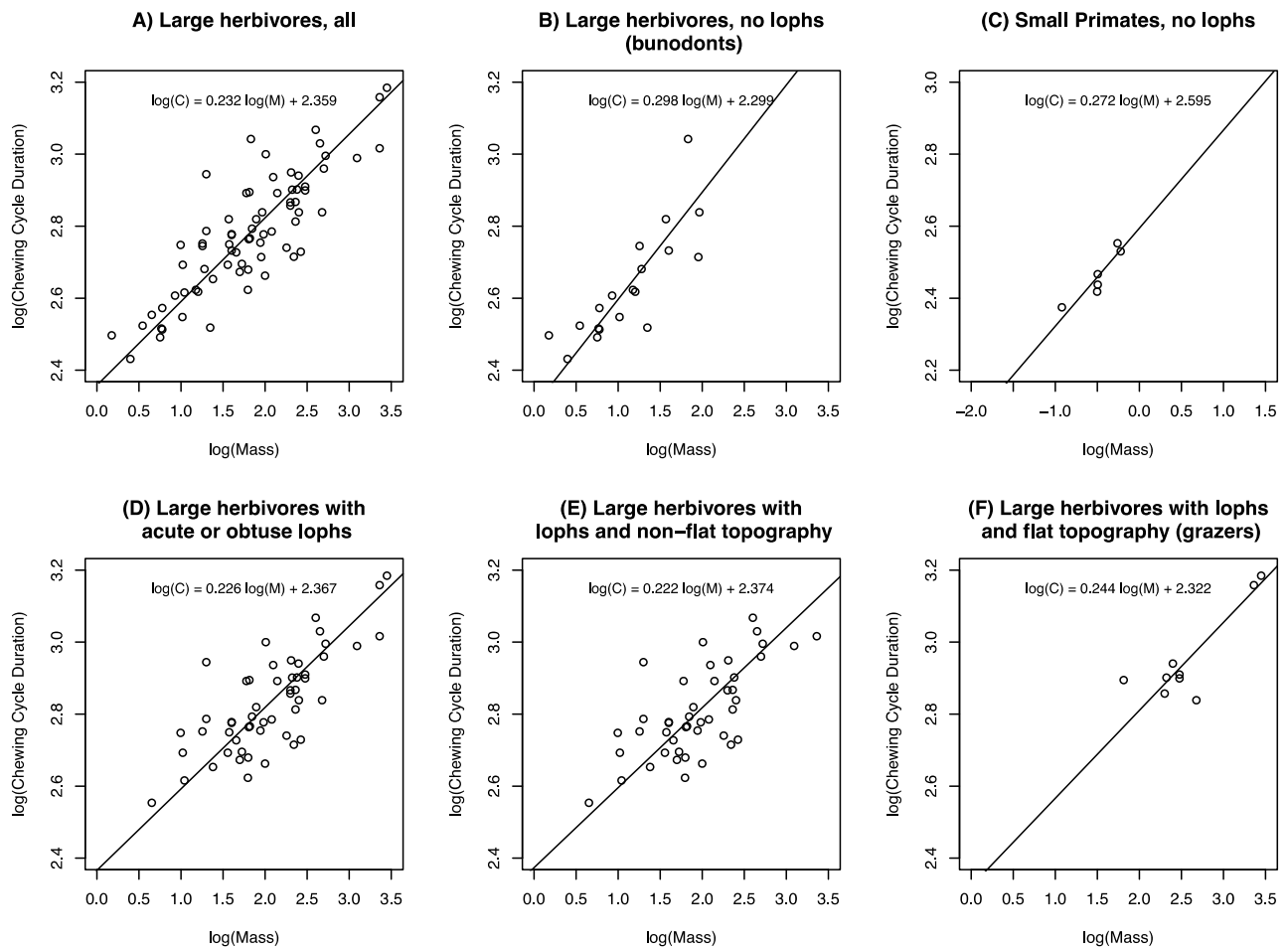


Figure S1. Scaling of chewing cycle duration with body mass, reduced major axis fit. (A) Large herbivores with all dental crown types, the line indicated reduced major axis fit; (B) regression fit only on those large herbivores that have no lophs; (C) Small Primates, none have lophs; (D) regression fit only on those large herbivores that have lophs; (E) regression fit only on those large herbivores that have lophs and *non-flat* occlusal topography; (F) regression fit on those large herbivores that have lophs and *flat* occlusal topography.

Table S4. Data used in the analysis. Chewing rates and body mass are from Gerstner and Gerstein (2008), dental traits are from Zliobaite et al. (2016) and new data.

Common name	Order	Family	Genus	Species	Mass (kg)	Chewing cycle duration (ms)	Acute lophs	Obtuse lophs	Occlusal topography
Giraffe	Artiodactyla	Giraffidae	<i>Giraffa</i>	<i>camelopardalis</i>	1240	976	0	1	0
Okapi	Artiodactyla	Giraffidae	<i>Okapia</i>	<i>johnstoni</i>	240	798	0	1	0
European bison	Artiodactyla	Bovidae	<i>Bison</i>	<i>bonasus</i>	300	793	0	1	1
Domestic cow	Artiodactyla	Bovidae	<i>Bos</i>	<i>taurus</i>	476,272	690	0	1	1
Yak	Artiodactyla	Bovidae	<i>Bos</i>	<i>grunniens</i>	250	872	0	1	1
Nilgai	Artiodactyla	Bovidae	<i>Boselaphus</i>	<i>tragocamelus</i>	180	550	0	1	0
Sitatunga	Artiodactyla	Bovidae	<i>Tragelaphus</i>	<i>spekii</i>	88	568	0	1	0
Nyala	Artiodactyla	Bovidae	<i>Tragelaphus</i>	<i>angasii</i>	45,4	534	0	1	0
Greater kudu	Artiodactyla	Bovidae	<i>Tragelaphus</i>	<i>strepsiceros</i>	252,5	690	0	1	0
Blackbuck	Artiodactyla	Bovidae	<i>Antilope</i>	<i>cervicapra</i>	36	493	0	1	0
Dama gazelle	Artiodactyla	Bovidae	<i>Nanger</i>	<i>dama</i>	63	478	0	1	0
Thomson's gazelle	Artiodactyla	Bovidae	<i>Eudorcas</i>	<i>thomsonii</i>	24	450	0	1	0
Saudi goitered gazelle	Artiodactyla	Bovidae	<i>Gazella</i>	<i>subgutturosa</i>	20	880	0	1	0
Springbok	Artiodactyla	Bovidae	<i>Antidorcas</i>	<i>marsupialis</i>	37,5	562	0	1	0
Impala	Artiodactyla	Bovidae	<i>Aepyceros</i>	<i>melampus</i>	62,5	420	0	1	0
Sable antelope	Artiodactyla	Bovidae	<i>Hippotragus</i>	<i>niger</i>	230	737	0	1	0
Arabian oryx	Artiodactyla	Bovidae	<i>Oryx</i>	<i>leucoryx</i>	70	621	0	1	0
Scimitar-horned oryx	Artiodactyla	Bovidae	<i>Oryx</i>	<i>dammah</i>	204	890	0	1	0
Gemsbok	Artiodactyla	Bovidae	<i>Oryx</i>	<i>gazella</i>	200	735	0	1	0
Addax	Artiodactyla	Bovidae	<i>Addax</i>	<i>nasomaculatus</i>	102	1000	0	1	0
Rocky mountain goat	Artiodactyla	Bovidae	<i>Oreamnos</i>	<i>americanus</i>	60	780	0	1	0
Dall's sheep	Artiodactyla	Bovidae	<i>Ovis</i>	<i>dalli</i>	10,5	493	0	1	0
Himalayan tahr	Artiodactyla	Bovidae	<i>Hemitragus</i>	<i>jemlahicus</i>	50	471	0	1	0
Alpine ibex	Artiodactyla	Bovidae	<i>Capra</i>	<i>ibex</i>	40	597	0	1	0
Markhor	Artiodactyla	Bovidae	<i>Capra</i>	<i>falconeri</i>	64	581	0	1	0
Goat	Artiodactyla	Bovidae	<i>Capra</i>	<i>hircus</i>	40	600	0	1	0
Barbary sheep	Artiodactyla	Bovidae	<i>Ammotragus</i>	<i>lervia</i>	66	584	0	1	0
Musk ox	Artiodactyla	Bovidae	<i>Ovibos</i>	<i>moschatus</i>	400	1169	0	1	0
Waterbuck	Artiodactyla	Bovidae	<i>Kobus</i>	<i>ellipsiprymnus</i>	220	519	0	1	0
Lechwe	Artiodactyla	Bovidae	<i>Kobus</i>	<i>leche</i>	96	599	0	1	0
Blue duiker	Artiodactyla	Bovidae	<i>Philantomba</i>	<i>monticola</i>	4,5	358	0	1	0
Elk	Artiodactyla	Cervidae	<i>Cervus</i>	<i>elaphus</i>	266	536	0	1	0
Chital	Artiodactyla	Cervidae	<i>Axis</i>	<i>axis</i>	53	496	0	1	0
Reeve's muntjac	Artiodactyla	Cervidae	<i>Muntiacus</i>	<i>reevesi</i>	11	413	0	1	0
Indian muntjac deer	Artiodactyla	Cervidae	<i>Muntiacus</i>	<i>muntjak</i>	18	565	0	1	0
Roe deer	Artiodactyla	Cervidae	<i>Capreolus</i>	<i>capreolus</i>	20	612	0	1	0
Moose	Artiodactyla	Cervidae	<i>Alces</i>	<i>alces</i>	450	1072	0	1	0

White-tailed deer	Artiodactyla	Cervidae	<i>Odocoileus</i>	<i>virginianus</i>	78,5	660	0	1	0
Reindeer	Artiodactyla	Cervidae	<i>Rangifer</i>	<i>tarandus</i>	125	864	0	1	0
Dromedary camel	Artiodactyla	Camelidae	<i>Camelus</i>	<i>dromedarius</i>	525	990	0	1	0
Bactrian camel	Artiodactyla	Camelidae	<i>Camelus</i>	<i>bactrianus</i>	500	912	0	1	0
Guanaco	Artiodactyla	Camelidae	<i>Lama</i>	<i>guanicoe</i>	120	610	0	1	0
Llama	Artiodactyla	Camelidae	<i>Lama</i>	<i>glama</i>	140	780	0	1	0
Alpaca	Artiodactyla	Camelidae	<i>Lama</i>	<i>pacos</i>	100	460	0	1	0
Hippo	Artiodactyla	Hippopotamidae	<i>Hippopotamus</i>	<i>amphibius</i>	2300	1039	0	1	0
Wild boar	Artiodactyla	Suidae	<i>Sus</i>	<i>scrofa</i>	22,3	330	0	0	0
Warthog	Artiodactyla	Suidae	<i>Phacochoerus</i>	<i>aethiopicus</i>	90	518	0	0	1
Collared peccary	Artiodactyla	Tayassuidae	<i>Pecari</i>	<i>tajacu</i>	19	480	0	0	0
Brazilian tapir	Perissodactyla	Tapiridae	<i>Tapirus</i>	<i>terrestris</i>	230	650	1	0	0
White rhinoceros	Perissodactyla	Rhinocerotidae	<i>Ceratotherium</i>	<i>simum</i>	2300	1440	0	1	1
Grant's zebra	Perissodactyla	Equidae	<i>Equus</i>	<i>burchellii</i>	200	720	0	1	1
Przewalski's horse	Perissodactyla	Equidae	<i>Equus</i>	<i>przewalskii</i>	300	813	0	1	1
Domestic horse	Perissodactyla	Equidae	<i>Equus</i>	<i>caballus</i>	65,0905	785	0	1	1
Asiatic wild ass	Perissodactyla	Equidae	<i>Equus</i>	<i>hemionus</i>	210	797	0	1	1
African elephant	Proboscidea	Elephantidae	<i>Loxodonta</i>	<i>africana</i>	2812,273	1530	0	1	1
Thick-tailed bush baby	Primates	Galagidae	<i>Otolemur</i>	<i>crassicaudatus</i>	1,5	314	0	0	0
Ring-tailed lemur	Primates	Lemuridae	<i>Lemur</i>	<i>catta</i>	2,5	270	0	0	0
Spider monkey	Primates	Atelidae	<i>Ateles</i>	<i>geoffroyi</i>	6	326	0	0	0
Japanese macaque	Primates	Cercopithecidae	<i>Macaca</i>	<i>fuscata</i>	15	420	0	0	0
Rhesus macaque	Primates	Cercopithecidae	<i>Macaca</i>	<i>mulatta</i>	3,5	334	0	0	0
Mandrill	Primates	Cercopithecidae	<i>Mandrillus</i>	<i>sphinx</i>	18	556	0	0	0
Sykes monkey	Primates	Cercopithecidae	<i>Cercopithecus</i>	<i>mitis</i>	5,65	310	0	0	0
De Brazza's monkey	Primates	Cercopithecidae	<i>Cercopithecus</i>	<i>neglectus</i>	5,85	328	0	0	0
Patas monkey	Primates	Cercopithecidae	<i>Erythrocebus</i>	<i>patas</i>	8,5	405	0	0	0
Guereza	Primates	Cercopithecidae	<i>Colobus</i>	<i>guereza</i>	9,9	560	1	0	0
Hanuman langur	Primates	Cercopithecidae	<i>Semnopithecus</i>	<i>entellus</i>	16	415	0	0	0
White-handed gibbon	Primates	Hylobatidae	<i>Hylobates</i>	<i>lar</i>	6	374	0	0	0
Siamang	Primates	Hylobatidae	<i>Symphalangus</i>	<i>syndactylus</i>	10,4	353	0	0	0
Human	Primates	Hominidae	<i>Homo</i>	<i>sapiens</i>	67,9	1102	0	0	0
Chimpanzee	Primates	Hominidae	<i>Pan</i>	<i>troglodytes</i>	40	540	0	0	0
Gorilla	Primates	Hominidae	<i>Gorilla</i>	<i>gorilla</i>	92,5	690	0	0	0
Orangutan	Primates	Hominidae	<i>Pongo</i>	<i>pygmaeus</i>	37	660	0	0	0